

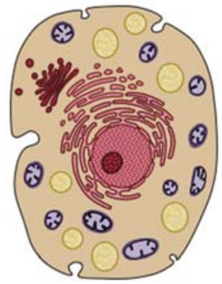
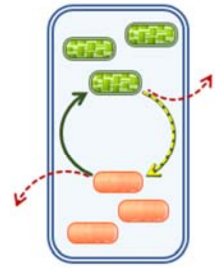

Principles of Biology

Edited Collection:

Eva Horne, Robbie Bear, and David Rintoul



Contents

Chapter 1 : Studio Biology: What is it?

Introduction

Welcome to Principles of Biology, Kansas State University's innovative introductory biology course. Because this course is almost certainly unlike any course you have taken before, we need to spend a little time to introduce it, and tell you why this course is a great way to learn about biology.

Unlike the traditional lecture & lab introductory biology courses at most universities, Biology 198 at K-State is a studio-format course, combining lecture and lab into the same class period. There are some unique things about studio courses, and especially this one. Our studio model involves 2 separate 2-hour sessions per week, with a maximum of 78 students in the studio; thus you will spend about 4 hours per week in the studio classroom. So it is important to understand that you are in a studio course, which is not a lecture, and not a lab, but is actually a hybrid of lecture and lab. Although it is an introductory course, it was developed with input from all the faculty members in the Division of Biology. There are usually two faculty members, two GTAs and one or more undergraduate practicum student instructors per 80 students in each section.

Why do we teach this course this way? Because we believe in education, and also in giving KSU students a lot of education for their tuition dollars. The studio format has been shown to be a very effective way for us to help you learn about biology. In fact, it is about twice as effective as the traditional lecture/lab course in terms of your learning and retention of the material. So that's why we teach it this way.

It is also unique in that the faculty members teaching this course can include anyone in the department, including full professors. Introductory science courses, in particular, tend to be taught by graduate teaching assistants here, and at other institutions. If they are taught by a full professor in Biology 198, many freshman students will not have another course taught by a full professor until their junior or senior year. At many of our peer institutions, introductory biology courses are taught with a single instructor lecturing to 500-800 students, accompanied by a lab taught solely with graduate students. That's a relatively inexpensive way to teach introductory science courses, but also a relatively ineffective way. If you take advantage of the significant resources (both personnel and material) that the Division of Biology devotes to this course, you will learn a lot of biology. Equally importantly, you will learn how to study and be successful in a university environment. That's another advantage of the studio format!

Course materials

Two items are essential to your successful learning in this course, both of which are designed to maximize learning in the studio environment. The first is the free electronic textbook, which you are reading now. The second is the Principles of Biology Studio Manual, which must be purchased from the KSU Biology Graduate Student Association. It may look like a lab notebook, but is actually something quite different. The studio manual is analogous to your lecture notes in a standard lecture class; it is simply YOUR record of what you do in the studio. What you see, do and hear during your time in class will be recorded in your Principles of Biology Studio Manual. More importantly, it is not analogous to a lab notebook in a lab class. You do not need to turn it in to be graded (just like nobody grades your lecture notes in a lecture class!). So please treat that studio manual, which is a required text for this course, like you would your lecture notes in any other class. Read it over before the next class, mark down any questions you might have, and make sure you get a copy of the notes from another student if you have to miss a studio class.

Course and testing structure

The course is divided into 7 units, each with four or five class periods that are devoted to those units. There are tests on all 7 units, and the dates for those tests can be found on your course syllabus (link). You will start with an Introduction to Science and Biology (including two classes on Evolution), then go immediately into the study of Ecology and Ecosystems. After gaining this large-scale perspective, you will move to the study of living things at the smallest scale (molecules and cells), and then move up to the organism level (Genetics, Energetics). The final two units are more traditional (Plant Biology, Animal Biology). The final exam, at the end of the semester, is not a comprehensive exam; it covers only the last unit (Animal Biology). But all of the learning that you have done in prior units will be very important in your understanding of the concepts covered in that final exam

The test questions are all written to evaluate your knowledge of the unit Objectives. More importantly, the objectives for each class period are provided to you at the very beginning of each section of the studio manual. So, if you want to know “What do I have to know for the tests?”, the simple answer would be “the Objectives for that unit”. You will gain an understanding of these objectives in many ways, not only from this electronic textbook, but from the studio exercises, the web pages for this class, and from discussions with your fellow students both inside and outside the classroom. In addition, we have prepared Study Guides that are also based on the Objectives. For each of the day’s Objectives, we provide a detailed listing of all the places (e.g. textbook, studio exercise, web page, or some combination of those) where you can get the information needed to master that Objective. If you spend your time in the studio wisely, and study with those Study Guides regularly (not just the day before the exam!), you should have a very clear understanding of the material that we think you should be learning in this class. Each question on each exam is written with one of those Objectives in mind, so it should be obvious that the Objectives are the key item on which to focus your efforts.

Your responsibilities

There will be readings in the textbook for every class day (except for the very first day of class); those reading assignments are listed in the Studio Manual, right after the Objectives for every class period. The textbook readings are an introduction to the topics for the studio exercises that day, so you need to read them BEFORE coming to class each day. In order to assure that you do the reading, there will be a short quiz over the reading material for every class period. By the end of the semester, the points for these quizzes add up to approximately the same value as a unit exam. The points should provide some incentive, but as you learn more about this course you should also figure out that learning in the studio classroom is more efficient if you have a good understanding of the material covered in the reading for that day. And more efficient learning in the classroom translates to better scores on the unit exams!

In addition, your instructors will track your attendance in the studio; attendance is not required in this class, but there is a participation bonus for being in class and working with others. Don't worry, if miss a class, if you get sick, or have to travel, because we have ways of accessing the computer material outside of class. The reasoning behind this attendance policy is quite simple. We have excellent data which prove that missing multiple classes is highly correlated with lower exam scores, and lesser learning and retention. We really want you to learn biology, but you can't do that if you are not in class. So, to make sure that you take full advantage of the learning opportunities in the studio, we strictly enforce this participation policy.

Your success in this course, both in terms of amount learned and in terms of a good grade, is assured if you understand the format of the course, do the assigned readings and attend the studio sessions faithfully, and spend at least as much time studying outside the classroom as you spend inside the classroom. You are responsible for learning, just as you are responsible in every class you take. But the difference in this class is that we do everything we can to provide the resources and the environment where learning is maximized.

Instructor responsibilities

Your studio instructors will deliver a brief (10-15 minute) introductory lecture at the start of each class day, and an equally brief wrap-up session at the end. In between those two lectures, you will be working with your fellow students on the studio exercises for that day. During that time the instructors will circulate in the studio, asking questions, answering questions, and generally helping you learn the material. Please take advantage of this incredible opportunity to interact, one on one, with your faculty and GTA instructors.

If you have a question, don't be shy. If you want to know if your class notes (i.e., the stuff you are writing in the Studio Manual) are accurate, ask an instructor. Their job is to help you learn the material, and they can help a lot more if they know what your questions and concerns might be.

Your studio instructors will also be responsible for grading the daily quizzes and recording those grades, usually in a course that they set up on K-State Online. If you are not familiar with K-State Online, don't worry. It is our course management system, and it is very easy to navigate. Your studio instructors will not be responsible for writing the biweekly unit exams. Since there are 10 sections of this course each semester, it is better (and more fair) if all students in all sections take the same exams. So, those exams are written by the course coordinator, and all exam questions are vetted by faculty members who are teaching in one or more sections in a semester. The first 6 unit exams are administered on Monday evenings (see syllabus for the exact dates), and the final unit exam is administered on Thursday morning during finals week. Grades for these exams will be recorded on K-State Online as well, so that you have ready access to your grade information.

Helpful hints

- Read the assigned material before coming to class.
- Don't skip class.
- Take advantage of the learning opportunities afforded in the studio (your fellow students, the instructors, the undergraduate practicum students, the studio exercises, etc.) every time you are in class.
- Take good notes and read over your notes in the studio manual within 24 hours after every class.
- Use the study guides and concentrate on the Objectives when you study for the unit exams.
- Study a little bit every day rather than cramming the day before the exams.
- Ask lots of questions, and be prepared to answer lots of questions.
- Don't fall behind, but if you do, make every effort to catch up as soon as possible.

Chapter 2 : Introduction to Science and Biology

What is Biology?

Biology is the scientific study of life. That statement naturally leads to the question: What is life? Surprisingly, that is a difficult question to answer in just a few words! Most textbook-level definitions of life are merely a list of characteristics. Anything with all of the characteristics is said to be alive. Here's a typical list:

Living things

- respond to the environment.
- assimilate and use energy from their environment.
- maintain a relatively constant internal environment, even as the external environment changes (homeostasis).
- reproduce (at the level of organisms) and can evolve (at the level of populations).
- are highly organized, relative to their environment.

These are general characteristics, and might describe all living organisms, even those which have not yet been discovered. However, characteristics could be modified, added, or removed from this list as we learn more about life. For example, all living things discovered to date are composed of one or more cells and have DNA as their hereditary/genetic material. Some textbooks include these characteristics in their definition of life as well. More importantly, the commonality of DNA as the genetic molecule in all known life forms is strong evidence that all living things on this planet are related (they have a common ancestor).

One productive way to study and understand living things is to recognize that there is a **biological hierarchy**, which is basically an organizational concept map allowing us to focus on various levels of life. This hierarchy (Figure 1) extends from atoms and molecules, through cells, tissues, organs, organ systems, organisms, populations, communities, and ecosystems all the way to the biosphere (Planet Earth and all the living organisms populating it). Biologists often focus on one or another of these levels, simply because it is far easier to study one level at a time. But all biologists recognize that there are many interactions between levels, and those interactions lead to some very interesting and important processes.

As you learn biology in the studio classroom this semester, you will begin to understand the details underlying the characteristics of living things. Remember, what you are learning about life is based on Science not opinion and conjecture. So, you will learn how organisms respond to the environment, and how bacteria, plants and animals reproduce. You will learn how reproduction is integral to the process of evolution. You will learn the structure and function of cells and tissues and organs, plus how energy is gained and used so that these organized structures can be produced and maintained. Hopefully you will come to the realization that life, in all of its diverse incarnations, is amazing. Which is why biologists continue to study it!

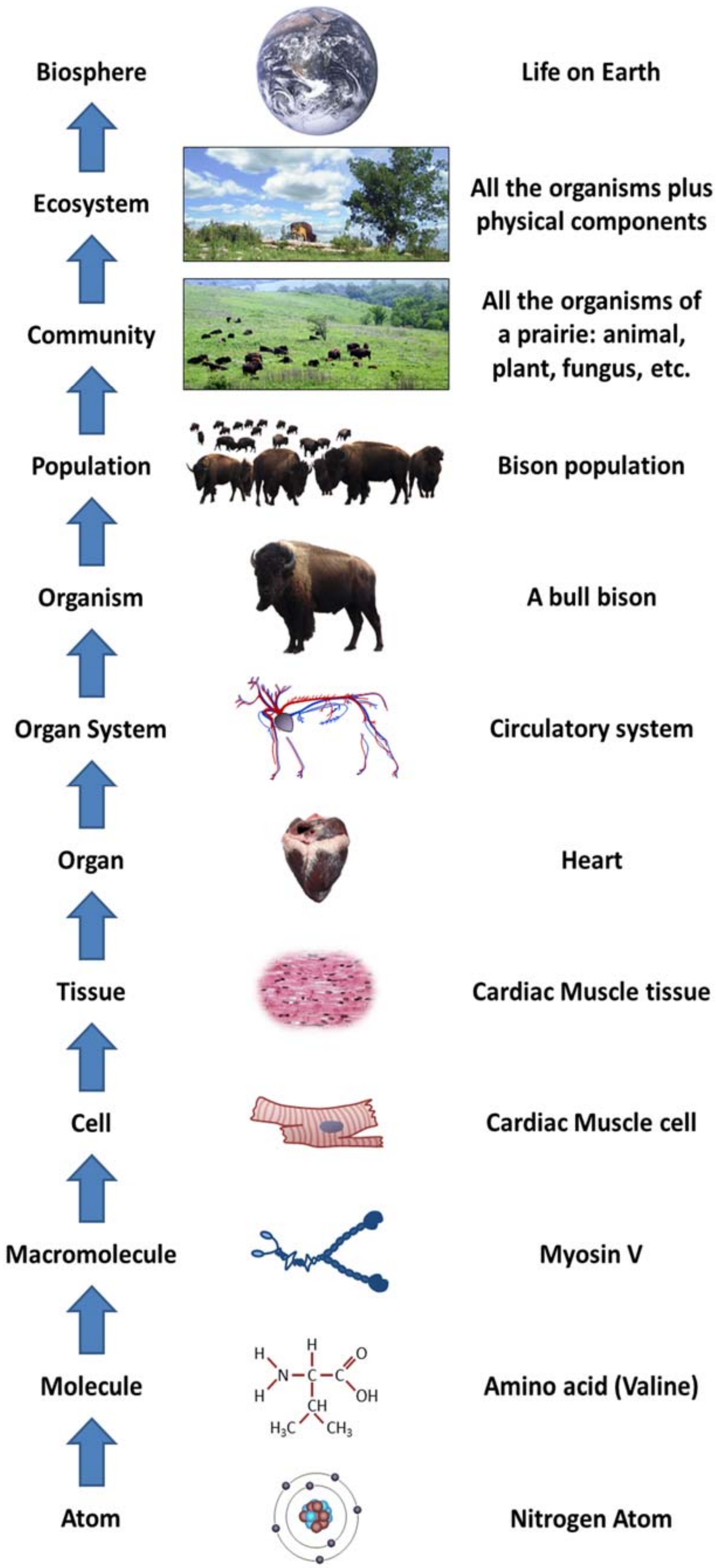

Figure 2-1: The hierarchical organization of life.

Science as a way of knowing

What is "Science"? Everyone probably has some idea of what the word means, but have you ever really thought about it? If so, here are some questions to consider:

- Is science a body of knowledge?
- Is it the same thing as "truth"?
- Is it a way to understand everything, or just a few things?
- Is it a process, and if so, can everyone do it? Or do you have to be highly intelligent, highly trained, or both, if you want to understand science?

Hopefully by the end of this course, or even by the end of this first module, you will have some good answers to those questions, and will be well on your way to thinking like a scientist (at least for this class!). Science is both a body of knowledge, and an evidence-based process for generating that knowledge. But science is also about a particular kind of knowledge - knowledge about the natural world and the process of "doing science" helps us gain additional understanding about the natural world.

Science

- requires interaction with the natural world in terms of observation, detection, or measurement.
- is objective, or evidence-based. Evidence generated by the scientific process must be available to everyone. Scientists generally don't just "take your word for it."
- requires independent evaluation and replication by others.
- leads to conclusions that are always *provisional*, i.e., they will be rejected or modified if new observations or measurements show that they are false.

There are, of course, other "ways of knowing". How do we know what we know? People who study knowledge (yes, there are such people, and they are in the branch of philosophy known as epistemology) often classify that knowledge based on the source of the knowledge. In mathematics and logic, for example, we can point to things that we know are "rationally true". In science, we focus on things that are "empirically true", i.e., based on evidence that we can see, hear, touch, etc. In religion, and, to a lesser extent, in history, we focus on "revelational truth", or knowledge that comes from another source that we accept as true, based on our assessment of the reliability of the source. So, the subjects that you might study at this university can depend on different sources for the knowledge that you will be gaining. In this class we will focus, as noted above, on objective evidence obtained from observations of the natural world, and we will use some very specific terms to describe how those empirical observations form the basis for scientific knowledge and understanding.

The process of science

The processes that generate scientific knowledge are known as the **scientific method**. But even as you learn this method, it is important to realize that this is not a set recipe that MUST be followed in all cases. The scientific method is best understood as a statement of the core logical principles underlying how science works. (Figure 2).

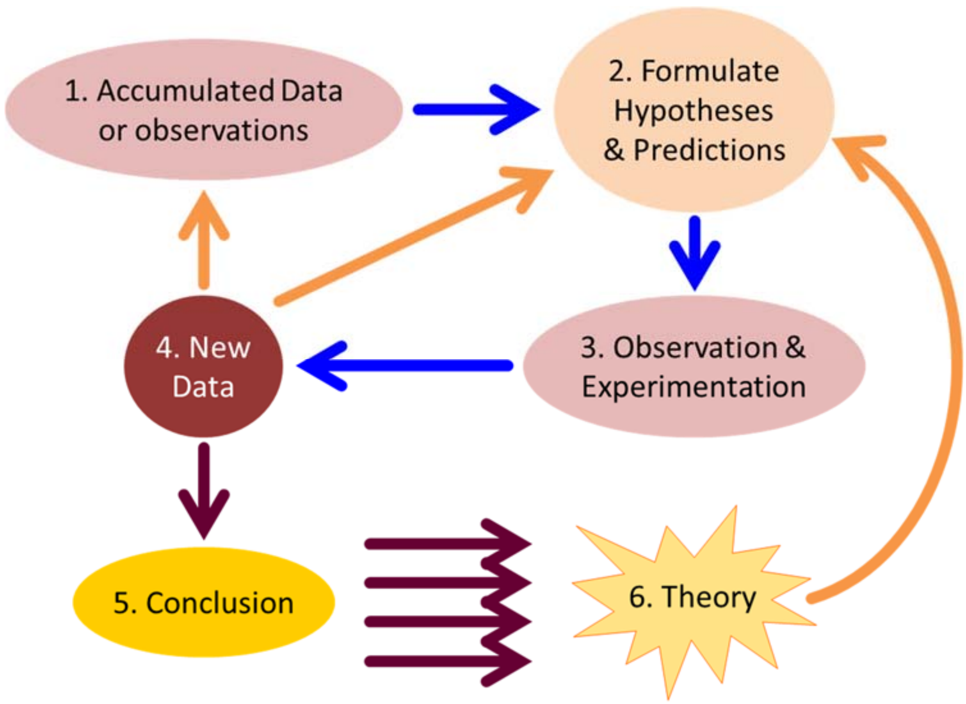

Figure 2-2: Basic steps of the Scientific Method.

All science starts with an **observation**, or set of observations, about the natural world. For example, you observe that some birds in the central United States fly in a flock but others don't. The next step is to formulate a **hypothesis** to explain that observation. A hypothesis is a statement that is an educated guess about the cause(s) of the observed phenomenon. "Educated guess" means that the hypothesis comes from your own experience and knowledge or from the published knowledge of others. For a hypothesis to be useful in a scientific sense, it must also have some additional characteristics. A scientific hypothesis must be **testable**, and it must be **falsifiable**. It does no good to generate a hypothesis that you cannot test in the real world. Thus, it would not be a scientific hypothesis if you stated that two of your pet Siamese fighting fish (bettas) spared all their fins and circle each other because a bird flying by the window told them to. That might be the actual explanation, but you can't test it nor prove that it is wrong (falsify it).

However, you might make the hypothesis that male bettas spread their fins and circle each other in order to defend a spot in the aquarium. You can test your hypothesis in two ways, by making more observations or by doing experiments. More observations might include watching to see if each fish spends more time in a particular part of the aquarium or measuring how closely one fish must get to the other to trigger the fin spreading display. This would be considered an **observational study** and is often used in ecological research. **Experiments** are manipulations of the system, followed by additional observations. In this case, for example, you might put one fish in a clear bottle and move it closer to the other, pausing every so many centimeters to make observations of behavior. Both of these approaches, using observations or using experiments, are scientifically valid, as long as your hypothesis is testable and falsifiable. Figure 2 illustrates that multiple tests of a hypothesis lead to an increase in accumulated data. Any test of the hypothesis, whether it supports or rejects the hypothesis, adds to our knowledge base.

Another important concept in the scientific method is **theory**. A **scientific theory** is a statement or set of statements that explains some aspect of the natural world and that is supported by substantial amounts of data from diverse lines of investigation. The statements that form a theory are NOT "guesses" of any sort but are often hypotheses that have been tested many times and never falsified. Therefore, a theory has predictive power and hypotheses generated from a theory can be tested. There are many theories in science; examples relevant to the study of biology include the germ theory, the cell theory, plate-tectonic theory, and the theory of evolution. All of them are well supported by incredible amounts of accumulated data and all of them are considered the best available explanation for a diverse set of observations.

In addition, theories also can lead to predictive hypotheses. In fact, one of the hallmarks of a theory is that it provides a solid framework for generating hypotheses. Scientists are confident in the explanatory power of theories, and thus are comfortable in using them to construct hypotheses, design experiments, and frame the interpretation of the data generated by those experiments. Just as a normal scientific hypothesis must be supported by new observations in order to be accepted, hypotheses generated from a theory must be supported by new observations if the theory is to continue to serve as the best available explanation for a natural phenomenon.

Another important aspect of the scientific method is that observations must be repeatable. Other scientists, working in other locations, need to be able to do similar experiments and get the same results. This makes science objective, rather than subjective. The history of science has thousands of examples where a new and exciting result was announced, but eventually forgotten when other scientists could not get the same result. Recent ones include the phenomenon known as “cold fusion” and the identification of a virus that was thought to cause Chronic Fatigue Syndrome (CFS). In these cases, the original observation was found to be flawed in some way, and subsequent work, either by the original observers or by others, revealed the flaws and falsified the hypothesis.

Experiments and controls

Experiments all start with an observation from which the scientist generates a testable hypothesis, followed by experiments based. Let’s look at one of the most famous experiments in all of biology as an example.

It was widely believed in ancient times that living things arose spontaneously if conditions were right. One of the observations that led to this belief was that molds, bacteria, maggots and other life forms appeared if one left a piece of meat out in the air for a while. This concept of spontaneous generation was tested in 1860 by Louis Pasteur, using the experimental setup diagrammed in Figure 3. Pasteur heated meat broth in glass flasks to a temperature where he imagined that no living things were left alive in the broth. If he left this broth out in the open, it developed active bacterial and mold growth, an observation which was consistent with the notion of spontaneous generation. But Pasteur, having recently learned about microbes, suspected that the mold and bacteria arose not from spontaneous generation, but from microbes present in the air. So, he devised a set of experiments to test this hypothesis: Living microbial cells present on dust particles in the air are the source of the living cells growing in the heated meat broth.

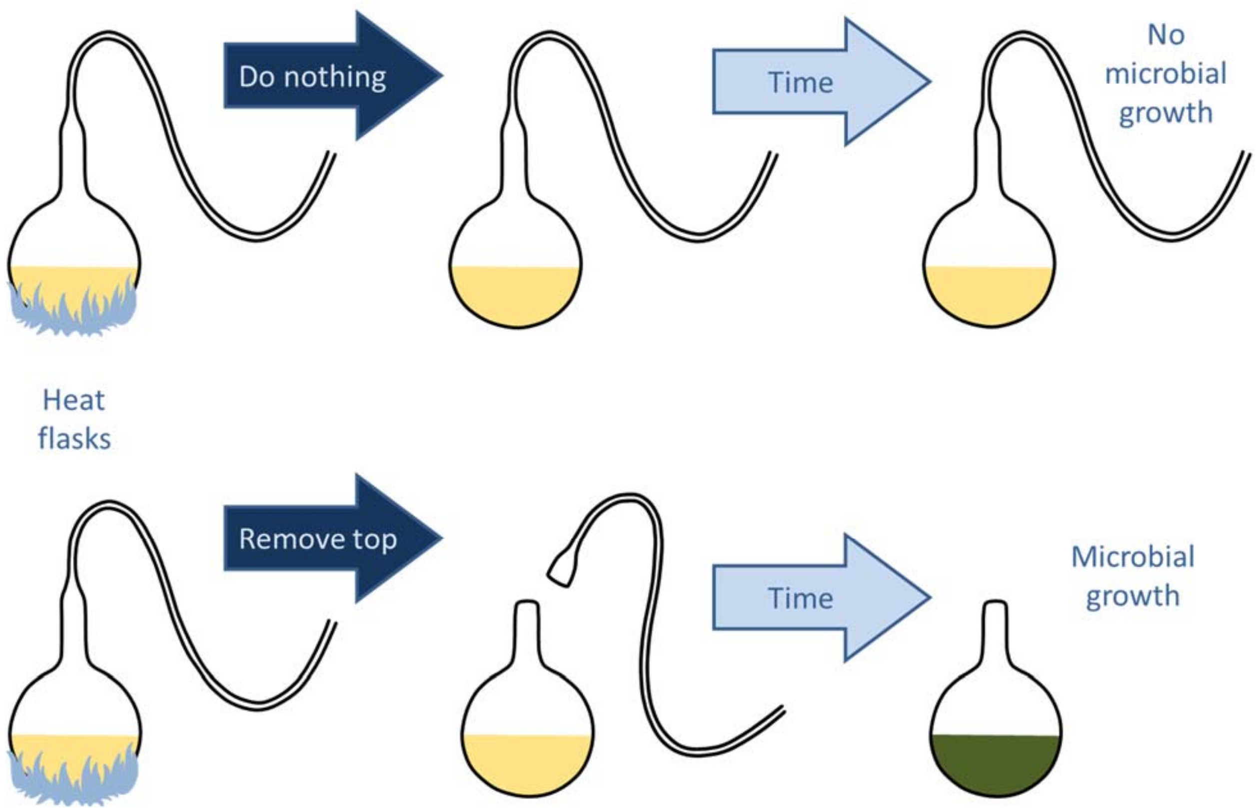

Figure 2-3: Pasteur's test of the hypothesis of spontaneous generation. Pasteur started with the observation that organisms (molds and bacteria) grew in meat broth even though it had been boiled. His hypothesis was that these organisms came from the air, rather than from spontaneous generation. He boiled the broth in flasks with long curved necks. Air could not enter past the fluid that was left in a U-shaped section of the neck of the flask. As a control he boiled broth in other long-necked flasks, but then broke the necks off so that air (and any microbes in that air) could fall on the broth. No organisms grew in the flasks with intact necks but were found in abundance in the flasks with the broken necks.

To test this hypothesis, Pasteur heated batches of broth in long-necked glass flasks until he thought the broth was sterilized, and also heated the necks of the flasks to allow him to bend them into a “S” shaped tubes. In some flasks the ends of the tubes remained open to the outside air, but dust settled in the trap in the neck of the flask and did not reach the surface of the meat broth. He broke neck off other heated flasks, allowing dust particles to settle on the broth. Then he observed the results. Just as importantly, he repeated the experiments several times to make sure that his observations were correct. In every experiment, microbes only grew in the open flasks, disproving the hypothesis of spontaneous generation and providing support for Pasteur’s hypothesis that the microbes are in the air.

An important component of experimental design is the concept of a **variable**. A variable is some condition of the experimental setup that can be manipulated by the experimenter. Ideally, the experimenter should change only one variable at a time (keeping all other conditions identical). This makes interpretation of the results a lot more straightforward. In Pasteur’s experiment, the manipulated variable was whether or not dust had access to the surface of the broth. In flasks that were left open, access was allowed. In the flasks that had an intact S-shaped trap in the neck, access was prevented.

Another important part of designing experiments are **controls**. A control (or control treatment) is a setup where everything is exactly the same except for the one variable being tested. So, Pasteur's experiment consisted of two treatments: incubation of broth in an open-necked flask (the experimental treatment) and incubation of broth in the S-necked flasks (the control treatment). All other variables (heating temperature, amount of broth, size of flasks, etc.) were the same in the experimental and control treatments. But it is not always possible to simplify a system so that there is only one variable different between treatments. In those cases, you might need multiple control treatments.

Chapter 3 : Introduction to Evolution and Natural Selection

Evolution. What is it?

The biological world is extremely diverse. In fact, that is one of the most powerful realizations that come from the study of biology, or even just from being an observant person in the world. Living things range from the microscopic bacteria to the immense blue whale. They have a diversity of lifestyles and metabolic capacities, from photosynthetic creatures who can make their own food from carbon dioxide gas, to predatory creatures, all the way to parasitic creatures who have some of the most complicated life styles of all. Within any one of these groups, there is also astounding diversity. Open any field guide, whether for birds, mammals, flowering plants, or mushrooms, and you will be confronted with an abundance of colors, sizes, shapes and behaviors. Even within a single species, say *Homo sapiens*, there is diversity. Look around any group of people and you will see a wide variety of skin colors, hair colors, eye colors, heights and weights. This diversity is a fact, and for many millennia, human beings have been trying to come up with explanations for that well-observed fact.

We won't go through the many explanations for the diversity of life that have been proposed and been discarded over the centuries. There are lots of places where you can read about that historical progression, and it is interesting, for sure. Rather, we will discuss the explanation most widely accepted by the current scientific community and show how this explanation is supported by evidence. That explanation is known as the **Theory of Evolution**. Theodosius Dobzhansky, a famous biologist, wrote in 1973 that "Nothing in biology makes sense except in the light of evolution". Every day, scientists around the world use the theory of evolution to generate hypotheses, interpret conclusions, and make contributions to scientific knowledge.

There are libraries and museums full of data and specimens demonstrating the wide diversity of life on earth, and that organisms change over time. Evolution is defined as "descent with modification". Basically, it is **change in the genetic makeup of a population over time**. There are a number of things that can cause genetic changes to a population and we will explore all but one of those in Module 3 (Genetics).

Here we discuss the concept most often linked with evolution, **natural selection.** Natural selection was first hypothesized in 1858 when two papers by Charles Darwin and an essay by Alfred Russel Wallace (J. Proc. Linn. Soc. 3, 45–62; 1858) first proposed natural selection as an agent of change over time. Darwin later went on to publish his book, *On the Origin of Species*, in 1859. Darwin and Wallace recognized that descent with modification was a common phenomenon, and that selection, whether natural or artificial (e.g. animal breeding) was an explanation for life's diversity.

Natural selection (aka adaptive evolution) is, as Darwin pointed out 150+ years ago, analogous to the process by which animal breeders produce animals with novel traits (aka artificial selection). For example, a pigeon breeder might notice that one of his pigeons has an unusually large ruff of feathers around its neck. He breeds this pigeon with another pigeon, and selects the pigeons with the biggest ruffs from among the offspring to be the parents of the next generation. After a few cycles of this, some of the pigeon offspring will have very unusual and pronounced neck ruffs, and will look nothing at all like the original pigeon ancestor in that regard (Figure 1). This common practice gets its name from the fact that the breeder *selects*, or chooses, specific animals to be the parents of the next generation. And it works; there are many examples where substantial changes in animal appearance or behavior, can be brought about in just a few generations by applying this artificial method of selection.

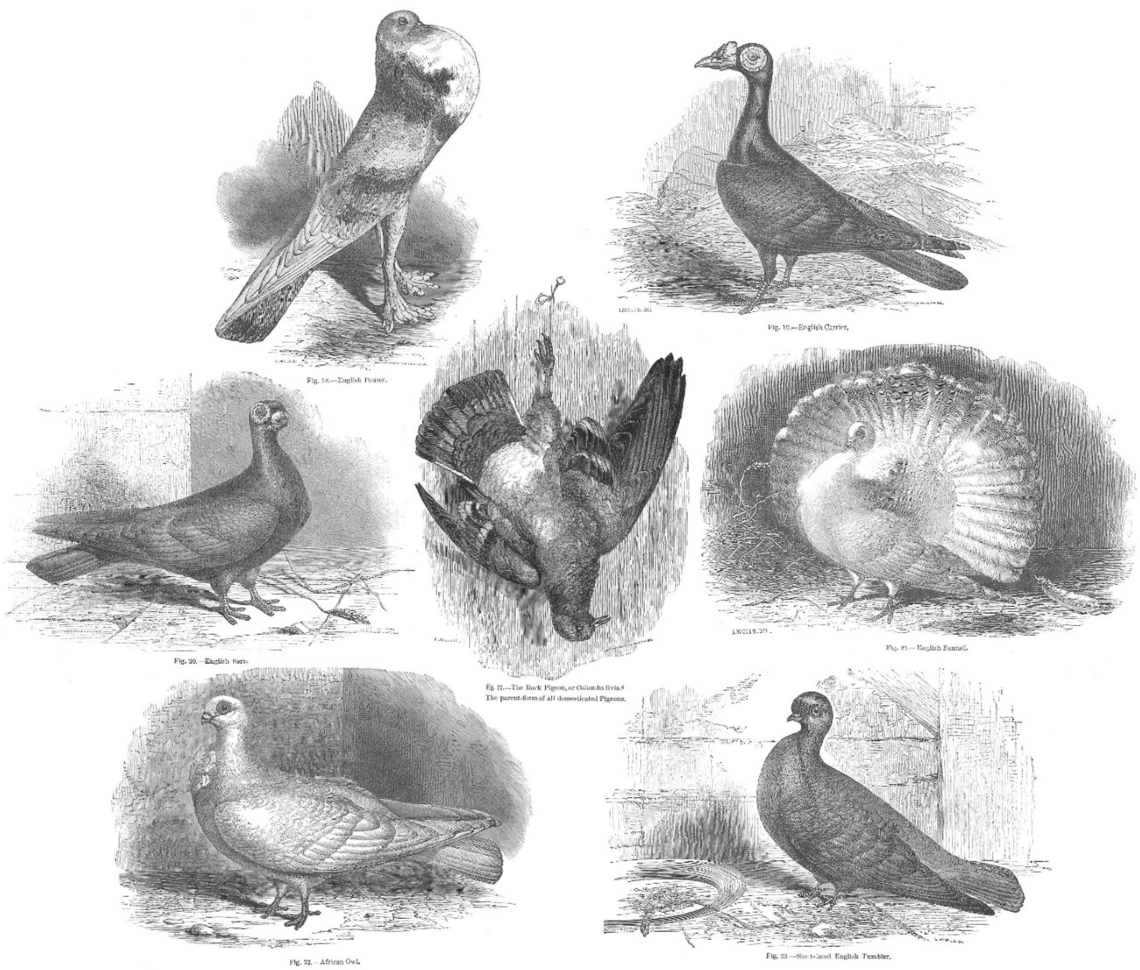

Figure 3-1: Darwin's pigeons. The common ancestor for all these fancy pigeons was the Rock Pigeon (center). By selecting for unusual morphological characteristics, pigeon breeders were able to develop all of these unusual pigeons, and many more.

Darwin recognized that three conditions were required for natural selection to cause change in a population. The first is that the variation observed in living things is due to heritable factors. In other words, there is *heritable variation* among the individuals in a population of organisms. We've already discussed the variation that can be observed in nature, both between and within species, and even within related individuals of a population. This variation is due to the expression of different versions of genes in different individuals, resulting in detectable differences in traits between those individuals. Variation is normal, and easily observed. Many of those variable traits are heritable, meaning that they are passed from one generation to the next. You have probably observed traits that are shared by the parents and offspring of many animals (humans included), things like eye color, hair color, height, etc. We now know that these shared traits are largely determined by shared copies of DNA molecules. On the other hand, some conditions are not heritable. For example, if you have a cat that lost its tail in a horrible and noisy accident involving a rocking chair and your 300-lb great-aunt, and if the cat has kittens, those kittens will have normal tails. The rocking chair might damage the cat's tail, but not its DNA. At the time of Darwin, the mechanisms of heritability were not known (he knew nothing about genes), but everyone understood that some traits were heritable, and others were not.

The second requirement for natural selection, is that not all of the individuals in a given generation will survive and reproduce to the same degree. This observation is supported by simple mathematics. If all of the fruit flies descended from a single pair survived and each produced a maximum number of offspring, in 25 generations (a single year) that population of flies would fill a sphere 96 million miles in diameter (more than the distance from the earth to the sun). Fruit flies have been around for lots longer than a year, and you can still see the sun, so obviously fruit flies do not all survive and reproduce.

The third condition necessitates that heritable variation can result in differences in survival or reproductive success. Again, there is abundant evidence for that. Inherited conditions that result in physical characteristics that make an organism more susceptible to starvation (i.e. the inability to digest protein completely), often mean that the affected individual will not survive or reproduce. Many heritable variations were not represented in the next generation because the individuals with those variations simply did not reproduce.

For the second and third conditions to exist, there must also be some sort of external force operating on the individuals. This "force" is the environment of an organism. Environments have abiotic (non-living) components like the weather or amount of nitrogen in the soil, or biotic (living) components like predators or competitors. Individuals with traits that allow them to do well under prevailing environmental conditions are better adapted to that environment and, therefore, have a higher **fitness** than other, less well adapted individuals. Fitness is a measure of how well individuals survive and reproduce in a particular environment. The **most fit** individuals are those that leave the most offspring. The trouble is that the environment is rarely stable, so individuals adapted to a wet environment may not do as well the next year if it is dry, while other individuals with other traits will do better.

The process of evolution is NOT random. The interaction of a organism and its environment leads to selection, and selection, by the very nature of the word, is not random. Just as an animal breeder chooses specific individuals as the parents of the next generation, the process of natural selection chooses specific individuals as the parents of the next generation, leading to evolution of the population. There are some important differences, however. In artificial selection, the breeder has a goal (e.g. to get a goat that produces more milk), and designs the breeding program with that goal in mind. In natural selection, there is no ultimate goal, and no plan; organisms are selected for their adaptation in a particular environment, which can (and often does) change. The process is unguided, in the sense that there is no goal in mind, but unguided is not the same thing as random.

Secondly, careful consideration of this process also disproves the notion that evolution equals progress toward a “better” organism. An organism that is better adapted to one environment can be very ill-adapted if the environment changes. In that situation, a “worse” organism, one that is rare in the first environment, is now the “better” one in the new environment. That is not progress, it is just change. In fact, some organisms become so well-adapted to their environments that they lose some of the complex structures or pathways that their ancestors had. Cave fish have no eyes, even though their ancestors did. Whales have no legs, even though their ancestors did. These highly-adapted organisms are actually less complex than the ancestors from which they evolved.

Finally, it should be clear that evolution is a change at the level of the **population**, and not at the level of the organism. Natural selection acts on individuals, but the result of selection is seen in the next generation. And this change is usually very gradual. As you work through the material this week, you will learn that even small differences in reproductive success can, over time, lead to large changes in the characteristics of organisms in a population. Small changes (one or two genes in individuals of the same species) are sometimes described as **microevolution**. The accumulation of microevolutionary changes over a long period of time can lead to **macroevolution**, the formation of new species.

Evidence for Evolution

There are multiple lines of evidence that support evolution as the explanation for the diversity of life. The following is not an exhaustive cataloguing of that evidence. Indeed, more evidence accumulates every day and not all the evidence comes just from biology. It requires a lot of time and many generations for enough microevolutionary changes to accumulate for a new species to be recognized. If the earth was too young, none of this could have happened. The sciences of physics and geology confirm that the earth is over 4.5 billion years old, which is plenty long enough for evolution to occur. The fossil record, the research subject of geology and paleontology, also provides substantial supporting evidence for evolution. The discovery of continental drift, and the development of plate tectonic theory, made sense of a lot of observations about both the fossil record and about populations of living organisms.

The fossil record

In science, radically new explanations can only be successful when the conventional explanations no longer explain all the observations. In the history of biology, this was the situation in the early part of the nineteenth century, when many interesting fossils were being discovered and carefully scrutinized. It soon became apparent that fossils were indeed the remains of once-living organisms, and that fossils in geologically younger strata (layers of rock) seemed to be both similar to and different from those in older strata. The fossil record showed that whole groups of organisms appeared and disappeared during the history of the earth. Others seemed to be much the same in rocks of different ages. Familiar organisms, particularly marine mollusks such as clams and snails, could be found in older rocks, but in many cases these organisms were not identical to the current organisms. Plant fossils told the same story.

Since Darwin's time the fossil record has become much more extensive. Gaps in the fossil record that were pointed out by Darwin's contemporaries have been gradually filled in. Indeed, the sciences of geology and paleontology, in combination with biology, have allowed scientists to make predictions about where, exactly, particular fossils in particular gaps should be found.

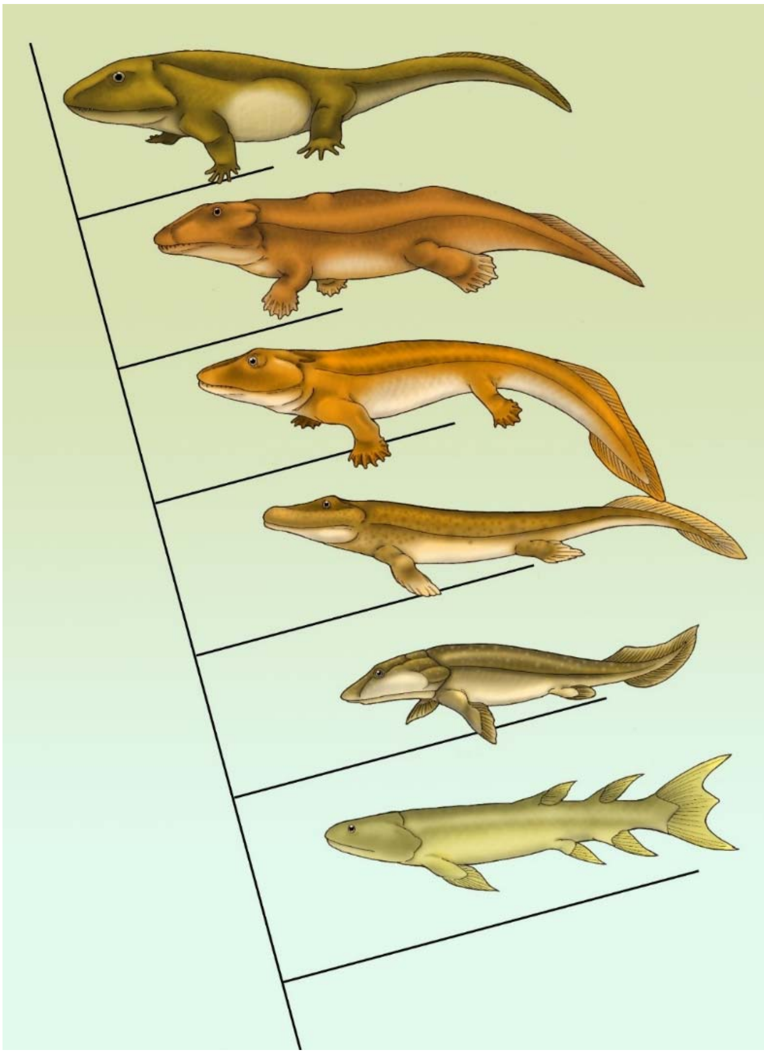

Figure 3-2: "Fishapod" evolution A cladogram showing the evolution of tetrapods, using the best-known transitional fossils. From bottom to top: Eusthenopteron, Panderichthys, Tiktaalik, Acanthostega, Ichthyostega, Pederpes.

A recent example of this was the discovery of fossilized remains of a creature that bridges the gap between fish and amphibians, which were the first four-legged vertebrates (aka tetrapods) to move onto land. The fossil record, coupled with genetic evidence from modern-day amphibians and fish, indicated that this transition to land occurred about 375-400 million years ago. But only fish fossils, or amphibian fossils, had ever been found. Logic dictates that there should be a transitional creature, which had characteristics of both fish and amphibians. It was reasoned that creatures such as this, if they existed, would probably live in shallow areas at the edge of seas or bays. Geologists knew which particular rock formations resulted from those sort of environments of that age, and so expeditions were dispatched to search for such fossils in one of those geological formations. These rocks were deposited in warm shallow tropical seas 375 million years ago, but are now, as a result of continental drift, located on Ellesmere Island in the Canadian Arctic. In 2004, fossils were found in those rocks that fit the profile of a “missing link”. The creature was named *Tiktaalik roseae* (Figure 2). The genus name for this “fishapod” comes from the name of a fish and was suggested by local Inuits on Ellesmere Island, and the specific epithet “roseae” honors an anonymous donor who helped fund these grueling expeditions to the high Arctic. *Tiktaalik* “fins” have basic wrist bones, but no digits, or fingers. It is truly a missing link, and its discovery stems directly from predictions made on the basis of previous scientific observations, in a classic example of the power of the explanatory framework known as the theory of evolution. Descriptions of the expeditions, and lots more about the incredible insights that have come from those fossils, can be found in a charming book called “Your Inner Fish”, written by Neil Shubin and published in 2008.

Comparative anatomy and embryology

Comparative anatomists have made many observations comparing structures in fossils to those in living organisms. For example, fossil skulls and modern skulls have remarkable similarities in the number and the position of the individual bones in the skull. Most of the bones in a fossil fish skull have counterparts, not only in modern fish skulls, but in fossil and modern amphibian skulls, or fossil and modern reptile skulls, and even fossil and modern mammal skulls. Occasionally the fossil record shows us when a skull bone is added or one is lost, and allows us to track progressive modifications in the positions of these bones on the skull surface. This is a great example of “descent with modification”.

The anatomy of modern organisms also reflects a common ancestry. The limbs of all tetrapods contain a similar number and arrangement of bones, even though the size and shape of the bones can vary greatly in different organisms. For example, the two bones in your forearm, the radius and the ulna, have counterparts in other mammals (Figure 3), in reptiles, in birds, and even in fossil dinosaurs and pleisiosaurs. If all these structures were specifically created for moving around in a different environment (e.g. water for the plesiosaur and air for the bird or bat), simple engineering principles would dictate that different structures would be more efficient in those different situations. Yet the same structures, endlessly modified, are found in all of them. The simplest explanation for this is that the organisms share a common ancestor in which that structure originated, and evolutionary mechanisms resulted in the modifications in size and shape that we see today. This phenomenon is known as **homology**. **Homologous structures** occupy similar positions and arise from a common ancestral structure, but have different functions.

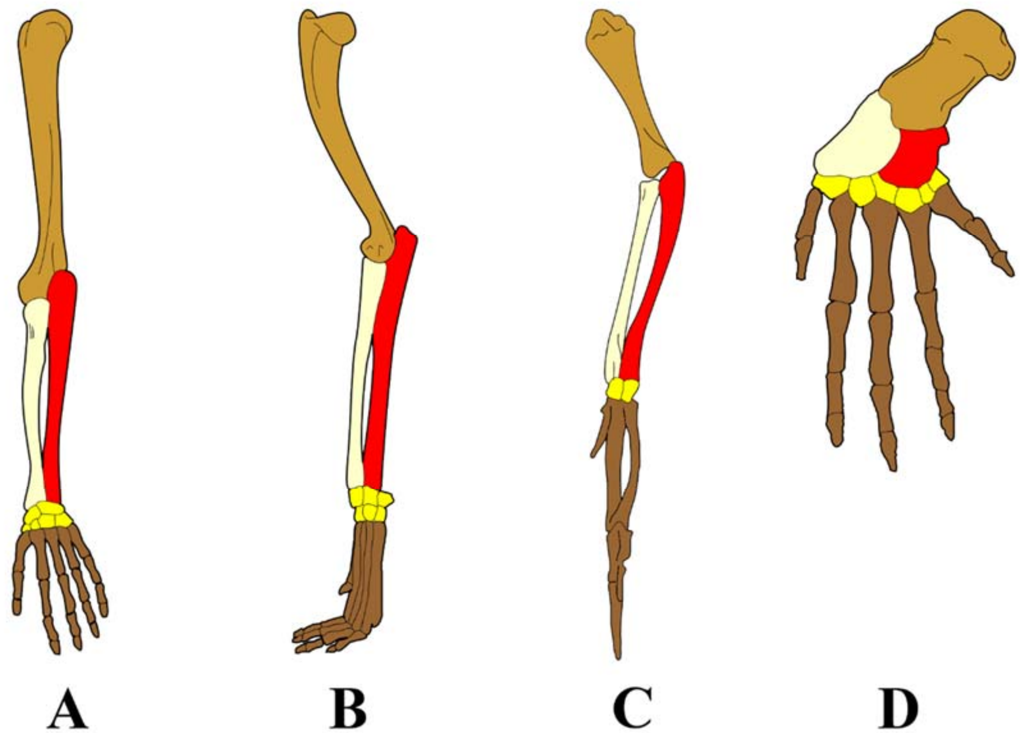

Figure 3-3: Homologous bones in the forelimbs of four vertebrates. A-human, B-dog, C-bird, D-whale. The various colors indicate bones of various groups (e.g. dark brown = bones of the fingers, yellow = bones of the wrist, red = ulna, beige = radius, and light brown = humerus).

Even vertebrates who have lost these limbs in the course of evolution (e.g. snakes) had similar structures prior to that evolutionary change. Figure 4 shows the fossilized remains of a creature (*Tetrapodophis amplectus*) that lived in what is now Brazil 120 million years ago. It had a snake-like body and may be the ancestor to all snakes, but it also had four small limbs. The forelimb shown in the figure clearly has the humerus, radius, ulna and hand bones that are found in modern vertebrates.

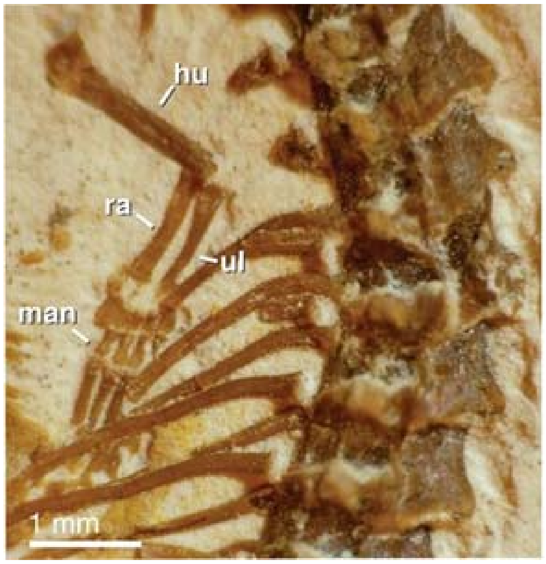

Figure 3-4: Forelimb bones in a fossil four-legged snake (Tetrapodophis amplectus) from the early Cretaceous (120 million years ago). Hu = humerus, ra = radius, ul = ulna and man = manus (hand).

Using the theory of evolution, embryologists predicted that homologous bones would arise from similar structures during the development of the embryo. For example, the forearm bone that we call the radius, which looks radically different in the forearms of a bat or a human or a mouse or a bird, would come from similar structures in the embryos of bats, humans, mice or birds. Those predictions also were found to be correct. So, homology strongly supports descent with modification.

In contrast, the wings of insects and the wings of bats do not have similar structures, although they have similar functions (to propel the organism through the air). These structures are said to be **analogous**. They share a function but do not arise from a structure that is found in a common ancestor.

Comparative biochemistry

One of the biggest surprises of modern biology came from the field of science known as biochemistry. Once biochemists started to unravel the mysteries of metabolism, the unity of life on this planet became even more obvious. Creatures with incredibly different morphologies, habitats, and lifestyles all seem to have incredibly similar metabolic pathways. Bacteria, bonobos, bats, and bananas all use a molecule known as ATP (adenosine triphosphate) to store and provide energy within their cells. The metabolic pathway known as glycolysis is found in all the organisms on the planet and the enzymes that are used in that pathway are similar in these diverse organisms. Again, this argues strongly for common ancestry and “descent with modification”. Once an ancient cell developed these metabolic pathways, there was no need to re-invent that wheel. It is somewhat ironic that some of the best evidence for a particular explanation for the diversity of life comes from the discovery of the unity of life at the molecular level.

Genetics and genomics

Besides ATP, another molecule common to all life forms on the planet is DNA (deoxyribonucleic acid). This molecule stores genetic information, so it is the molecule of heredity. Its role in heredity also means that it can be modified under some circumstances, thus giving rise to the variations described above. Darwin knew nothing about DNA when he proposed his theory in 1858. His ideas about how traits were passed from generation to generation were, in fact, spectacularly wrong. The mechanism of heredity was first proposed by Gregor Mendel in 1866 and expanded by many others in the early part of the 20th century. In fact, the first 4 decades of the 20th century were the years when the two seemingly unrelated fields of genetics and evolution were united. This Neo-Darwinian synthesis, starring Theodosius Dobzhansky, Ernst Mayr, and George Gaylord Simpson, resulted in modern evolutionary theory, and allowed scientists from both genetic and evolutionary backgrounds to work together to make and test predictions.

The elucidation of the structure of DNA by Watson and Crick in 1953, followed soon by the breaking of the genetic code, provided even more evidence for descent with modification. DNA functions as a repository of information. For the information to be used to build a cell or an organism, it must be read and translated into different molecules. The processes and the enzymes that do this work of reading and translating are virtually identical in all living creatures on the planet. The genetic code was, perhaps prematurely, called the "universal" genetic code for precisely that reason. It is translated identically in almost all organisms that have been discovered to date. Once again, this is a strong argument for common ancestry and descent with modification.

But the really impressive outcome of the fusion of molecular and organismal knowledge comes from the study of the structure of genes, and genomes, at a detailed level. Incredibly, scientists have discovered molecular fossils of a sort – stretches of DNA which are not used in modern organisms, but which remain in the genome as a record of functions in the past. For example, chickens don't have teeth, but they have genes for tooth proteins, turned off long ago, still lurking in their genomes. Those genes can be turned on under the right conditions, producing toothy structures, which were last seen in dinosaurs, the extinct ancestors of modern chickens. There is no good explanation for these observations, other than descent with modification. Similarly, detailed analysis of the DNA of organisms, including some now long-dead organisms like mammoths and Neanderthals, allows scientists to test predictions about common ancestry, and gain insights into the course of evolutionary change in all organisms. In fact, evidence from analysis of DNA, and other molecules, has allowed us to fine-tune our hypotheses about ancestry and relationships throughout the biological world.

Chapter 4 : Taxonomy and Phylogeny

Taxonomy

Observations about the similarities of and differences between the life forms around us have a long history. Aristotle (384-322 B. C.) was the first to write about attempts to classify animals into groups, and his classification scheme was the standard for many centuries. There have been many classification schemes throughout the centuries that have used many different criteria for separating living things into different groups. “How is this thing different from this other thing?” has been the focus of many scientific endeavors. But, as Aristotle recognized, it is just as important to ask about the similarities, and not focus solely on the differences.

We use the words **taxonomy** or systematics to describe the activity of classifying and naming living things. There are many ways to divide living things into groups. Some of these schemes are based on habitat, e.g. water-dwelling creatures vs. land-dwelling creatures or aerial-dwelling creatures. Others are based on internal characters. For example, Aristotle’s two most basic groups were those with blood and those without blood, a grouping scheme that coincidentally neatly separates most of the vertebrates from most of the invertebrates. But most schemes have been based on **morphology**, they physical structures of an organism, such as size, shape, number and proportion of appendages, etc. This sort of classification seems to be easy enough to do, but, as you will see later in this chapter, it can lead to some interesting mistakes.

Finally, it is important to understand that **all classification schemes should be viewed as hypotheses**. Like any hypothesis, a classification scheme should change, or even be discarded, if new observations contradict the original hypothesis.

A brief history of taxonomy

After Aristotle, there was not a lot of progress in taxonomy for many centuries. In fact, there may have been negative progress for some of that time, as Aristotle’s system was brushed aside or forgotten. But in the 1700’s Carolus Linneaus, a Swedish biologist, developed a system of biological classification that still underlies the system used today. His big contribution to the discipline was to introduce the concept of using two names to describe the smallest unit of classification, the *species*. In the Linnean system, every organism has a unique “scientific name”, consisting of a specific epithet preceded by a name for the next highest level of classification, the genus (plural = genera). Higher levels of classification included, in order above the genus, family, order, class, phylum, and kingdom. Subsequently another top level, the domain, was added to this hierarchy, giving us the classification scheme shown above (Figure 1). This bald eagle has the scientific name *Haliaetus leucocephalus*. There are seven other members of the genus *Haliaetus*. The genus is placed in the Family Accipitridae, in the Order Accipitriformes, in the class Aves, in the Phylum Chordata, in the Kingdom Animalia, and in the Domain Eukarya.

Biologists refer to a group of organisms, at any level, as a **taxon** (shorthand for taxonomic unit, plural = taxa). Thus a species is a taxon, as is a Genus, or a Family, or an Order, etc.

Domain - Eukarya
Kingdom - Animalia
Phylum - Chordata
Class - Aves
Order - Accipitriformes
Family - Accipitridae
Genus - Haliaetus
Species - leucocephalus

Figure 4-1: Taxonomic information for the Bald Eagle.

There are an estimated 8-9 million species on our planet. Every organism that has been described fits somewhere in this classification scheme. You can explore this in much more detail at the Tree of Life website. There you will find information on the thousands of species that have been described and named, as well as their currently assigned place in the taxonomic scheme. It is also worth pointing out that the basic unit of this scheme, the species, is not a well-defined term at all. There are multiple definitions of species that you can find with just a minimal bit of effort, and none of them is entirely satisfactory. Just as we learned about the definition of life, it is sometimes difficult to pin down an exact point on a hierarchy. As you will see from the material below, the problems with a definition of species might be related to the fact that evolution is ongoing, and that some groups of organisms are at different points on an evolutionary path at the present time.

However, if we ignore the vexing issue of figuring out a widely-accepted definition for "species", it is clear that a system based on this unit has several advantages. One of the immediate advantages of the Linnean system was that it allowed biologists to bypass the often-confusing different common names that are used in various parts of the world, or in various languages. For example, the animal that is known as a moose in North America is called an elk in Europe. But when you refer to this creature by its scientific name (*Alces alces*), there is no confusion. That is why scientific papers always include the two-term scientific name for a species. The hierarchical nature of the Linnean scheme is also useful, allowing us to easily understand the amount of similarity at different levels in the scheme. For example, organisms in the same genus can be very similar to each other, and may even be difficult to tell apart unless you are an expert. The similarity becomes less apparent for higher taxa. The class Aves includes the Bald Eagle mentioned above as well as your pet parakeet, which may screech like an eagle, but which is otherwise not very similar to an eagle at all.

The original Linnean taxonomy was based primarily on external morphology. It also relied on the obvious fact that organisms are related to each other in many ways, and that some seem more closely related than others. However, a system based solely on morphological similarities and differences can lead to some interesting classification errors. For example, Linneaus had one Phylum named Vermes (Latin for "worms"). This obsolete taxon included animals that we now classify with the mollusks, others that we now classify with the vertebrates, and still others that we now classify with crustaceans, as well as those that are still classified as worms. This reinforces two aspects of taxonomy that are important to remember. The first is that taxonomic classification schemes are merely hypotheses, and should be discarded or modified if newly obtained information is not consistent with that hypothesis. The second is that classification schemes based only on one type of information (in this case, external morphology) can be quite mistaken. Using more than one type of information will lead to better and more stable taxonomies.

Prior to Darwin's time, classification was merely cataloging, and the cataloging system used morphology as the key characteristic for determining relationships. The concept of evolution provided a different way of looking at classification. Besides being similar in size or shape, two organisms that were most closely related should have a common ancestor in the more recent past than would be the case for two less closely related organisms. The evolutionary history of the taxa was valuable and necessary information in this approach. The word for the determination of the evolutionary history of a species or group of species is **phylogenetics**, and the hypothesized evolutionary history of a species or group of species is a **phylogeny**. It quickly became clear that a taxonomic scheme that reflected phylogeny would be better than the arbitrary morphology-based schemes of the past. However, at the time of Darwin, and for many years thereafter, it was not exactly easy to discern the evolutionary history of organisms. So the development of a true phylogenetic taxonomy took a long time to develop, and, indeed, it is still being developed.

Taxonomy should reflect phylogeny

The current approach to determining relationships between two (or more) groups of organisms is the construction of what are called **phylogenetic trees**. Phylogenetic trees are hypothesized reconstructions of evolutionary history. They depict arrays of extant (currently living) organisms at the tips of the branches, with common ancestors located at the branch points (Figure 2). A, B, C, D, and E in this diagram are the species being considered. The vertical axis represents the passage of time. In some cases, ancestors are known species from the fossil record, but in most, they are not. A common ancestor for all these organisms is the branch point above the root of the tree, known as the **most recent common ancestor** (MRCA). The left tree depicted here was drawn with square branches and the right tree with V-shaped branches, but there is no difference in the hypothesized relationships between the organisms in the two trees.

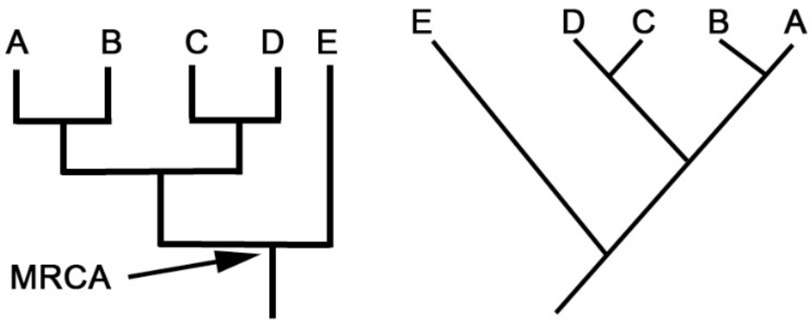

Figure 4-2: A simple phylogenetic tree. MRCA = Most recent common ancestor

Another critical point about these trees is that if you rotate the structures, using one of the branch points as a pivot, you don't change the relationships. So just like the two trees above, which show the same relationships even though they are formatted differently, all of the trees in Figure 3 are identical in terms of depicting the relationships between the species A, B, C, and D. If you don't see how that is true, follow the branching pattern between one species and another on each of the trees. You should see that the branching pattern is the same regardless of the order of the organisms from left to right across the tops of the trees.

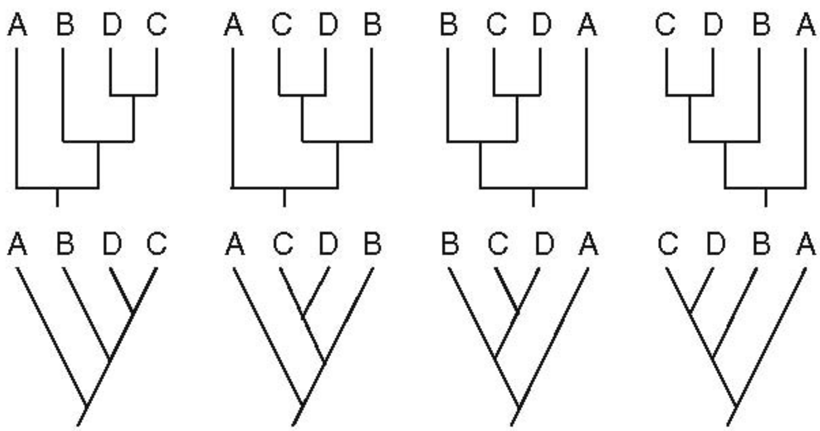

Figure 4-3: Different depictions of the same phylogenetic tree. All of these depict the same relationships between the organisms A, B, C and D.

To generate these tree structures, taxonomists use multiple characteristics to compare organisms, including external morphology, internal anatomy, behaviors, biochemical pathways, etc. In addition, the development of a method called **cladistics** has revolutionized taxonomic thinking, and cladistics also depends on an understanding of evolutionary relationships. A **clade** is a group of organisms that consists of a common ancestor and all its descendants. For example, birds (including the bald eagle and your parakeet AND their ancestors (including one group of dinosaurs) are a clade. Clades can contain any number of species, but that number must include all the descendants of a common ancestor. In the example above, A, B, C, D and E, as well as the ancestors indicated by the branch points and the MRCA, are a clade. A and B, plus their single common ancestor, are also considered to be a clade. The graphical representation of the relationships between organisms in a clade is called a **cladogram** and, for the purposes of this class, cladograms are essentially the same as a phylogenetic tree. Cladograms are just most often draw with V-shaped branching points. The important things to remember are 1) organisms are related, and 2) that we can represent our hypotheses about these relationships with tree structures.

Cladistics relies on classifying characteristics of organisms as either **ancestral** or **derived**. Ancestral characters are inherited attributes that resemble those of an ancestor to the group. Derived characters are features that are different from features found in the ancestor. But how do you know which features are ancestral, and which are derived? For now, you can assume that characters shared by all the organisms in a group are probably ancestral and that characters not shared by all the organisms in the group are derived. Lists of characters are generated, and used to construct a cladogram.

The best way to illustrate this process is with an example or two. Here is a table with some characters in rows and some organisms in columns. If there is an "X" in the column for an organism, the organism has that particular characteristic.

Character	Lamprey	Antelope	Bald eagle	Alligator	Sea bass
Lungs		X	X	X	
Jaws		X	X	X	X
Feathers			X		
Notochord	X	X	X	X	X
Gizzard			X	X	
Hair		X			

Which character is common to all these organisms? Obviously, it is the notochord. Assume that is the ancestral condition, and thus it should characterize the oldest ancestor at the base of any cladogram that you construct. Now you need to determine what the first branch in the tree is based on. That would be the character shared by all but one of these organisms, the presence of jaws. If you continue this process, adding a branch to the tree to depict groups that have, or do not have, a character, you will generate the cladogram in Figure 4. Note that ancestral and derived traits are relative. For example, "lungs" is an ancestral trait for the clade that includes eagle, alligator, and antelope, but is derived when compared to bass and lamprey.

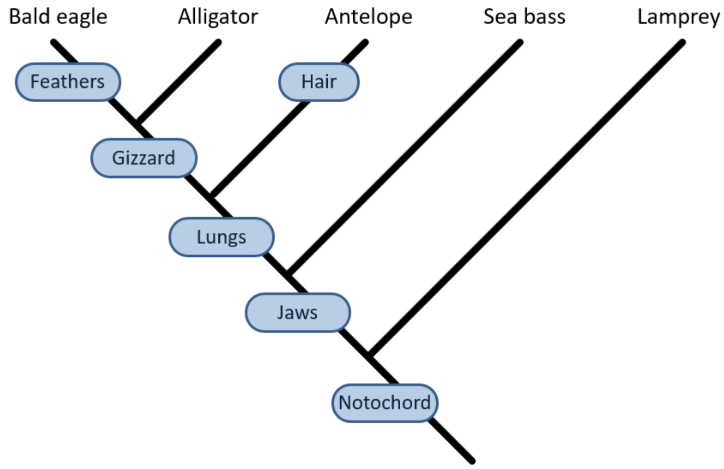

Figure 4-4: A cladogram constructed from the data in the table above.

Here are a few other things to remember about cladograms:

The organisms along the top of a cladogram are not ordered in any particular way, and are not ancestors of each other. The order does not imply any sort of ranking from “primitive” to “advanced”. As discussed in the previous chapter, evolution is not synonymous with progress and the patterns of branching are the important information in these diagrams.

The most closely related organisms have the most recent common ancestor, which is determined by counting the branch points backward from the organisms aligned across the top. For example, the bald eagle and the alligator have a more recent common ancestor than the alligator and the antelope, so the eagle and the alligator are more closely related than the alligator and the antelope.

The lines between branches represent time, but in most cases the length of these lines is not directly related to the length of time involved between the branch points. Some representations of cladograms include an axis where time can be deduced, but if there is no such axis, do not assume that a longer line represents a longer amount of time.

There are many ways to represent a cladogram, and many of these may look different, but will actually be identical. For example, the two cladograms shown in Figure 2 depict the same set of relationships, even though one is based on squares and the other is diagonal in nature. In both cases organism C is more closely related to D than B is to C.

Cladograms can be generated from any set of inherited characteristics. But they become powerful tools, both for understanding the world and for generating hypotheses, when they include DNA sequences. Because DNA is the molecule that produces heritable traits, comparing DNA sequences from different organisms is very useful in determining phylogenetic relationships. The development of DNA sequencing technology has resulted in an explosion of new and exciting discoveries about phylogeny.

Morphological traits, such as those used to construct the cladogram above, can be preserved in the fossil record, but DNA generally is not preserved. However, since we know that your DNA was inherited from your parents, and your grandparents, etc., we can predict that DNA sequences from related individuals would contain evidence of that relatedness. These sorts of "molecular fossils" can also be used to produce and refine cladograms.

"This view of life"

It is important to also understand that phylogenetic trees are **nested hierarchies**, i.e., any individual set of branches is also part of a larger set of branches (Figure 5). The clade containing the eagle and the alligator nests within a clade that also contains the antelope, and that clade nests within another clade, and another, etc. The hypothesis of descent with modification (i.e. evolution) absolutely predicts that the evolutionary history of organisms would be represented by a set of nested hierarchies. Cladistic analyses, particularly those based on DNA sequences, give results consistent with this prediction of Darwin's theory.

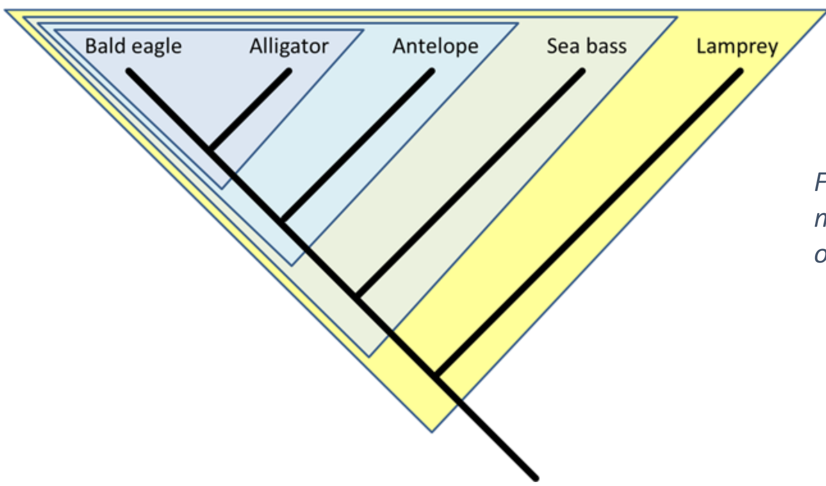

Figure 4-5: Cladogram showing a nested hierarchical arrangement of organisms.

If we continue backward in time from any tip of any branch of the phylogenetic tree above, we soon realize that all clades have a common ancestor at some point in the distant past. DNA evidence supports and strengthens this interpretation. You can look up any number of historic (Figure 6) and current phylogenetic trees and see that, while the details of the arrangements of the various branches may change, the fundamental conclusion, that all life on this planet came from a common ancestor, is a consistent feature. Indeed, as new observations are made, particularly in the realm of DNA sequence data, this conclusion has become increasingly well-supported.

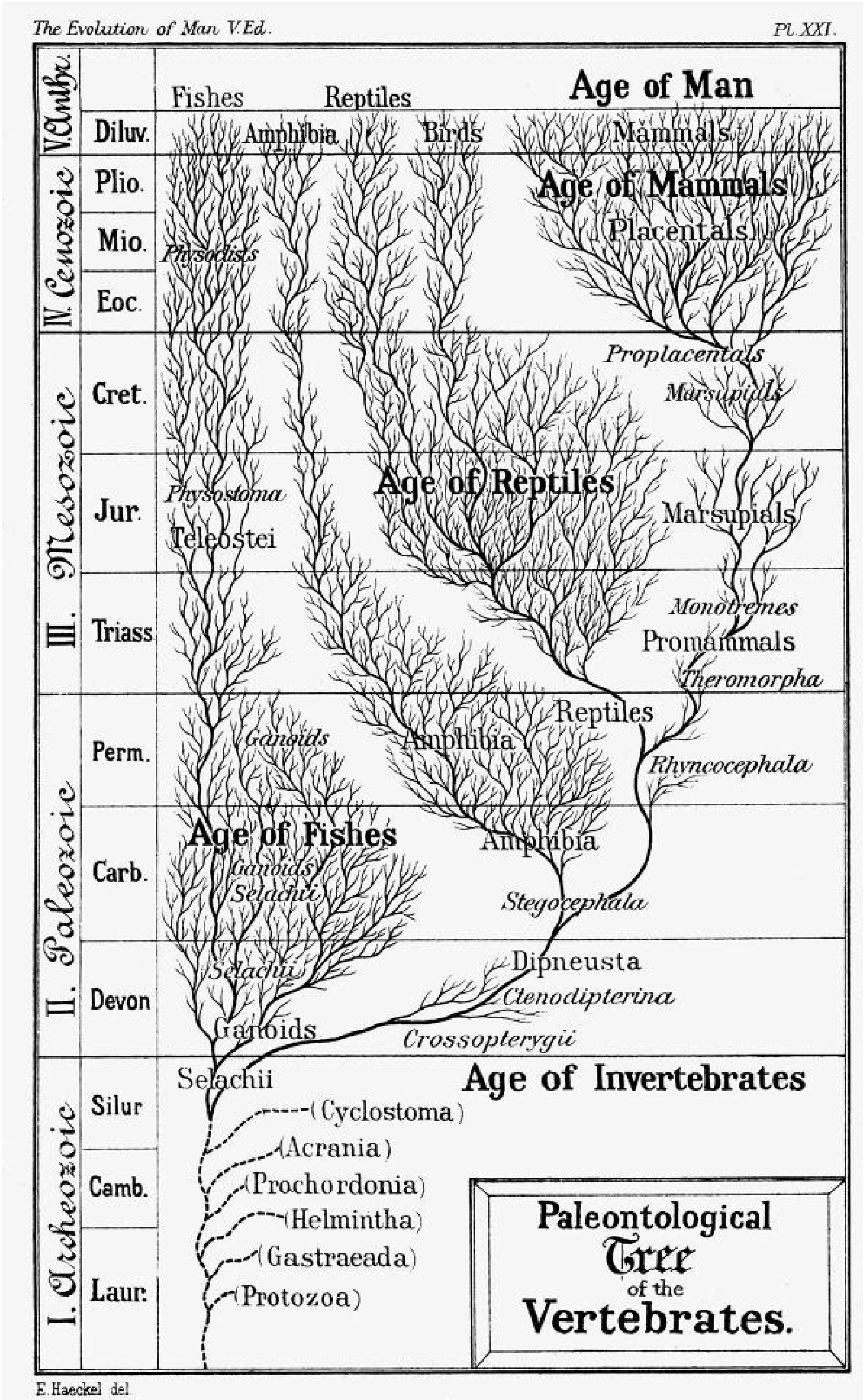

Figure 4-6: One of the earliest depictions of a phylogenetic tree by Ernst Haeckel in 1879.

The current most widely accepted tree has all living forms divided into three major Domains, Bacteria, Archaea, and Eukarya. The evolutionary relationship between these largest taxa is shown in Figure 7. Note that current data support the idea that the Eukarya (including humans) are more closely related to Archaea than they are to Bacteria. Archaea and Eukarya have a more recent common ancestor compared to Bacteria and Eukarya. Each of these Domains can be further subdivided into Kingdoms, Phyla, Classes, Orders, Families, Genera, and Species. For example, humans (*Homo sapiens*) are in the Domain Eukarya, Kingdom Animalia, Phylum Chordata, Class Mammalia, Order Primates, Family Hominidae, Genus *Homo*, and Species *sapiens*.

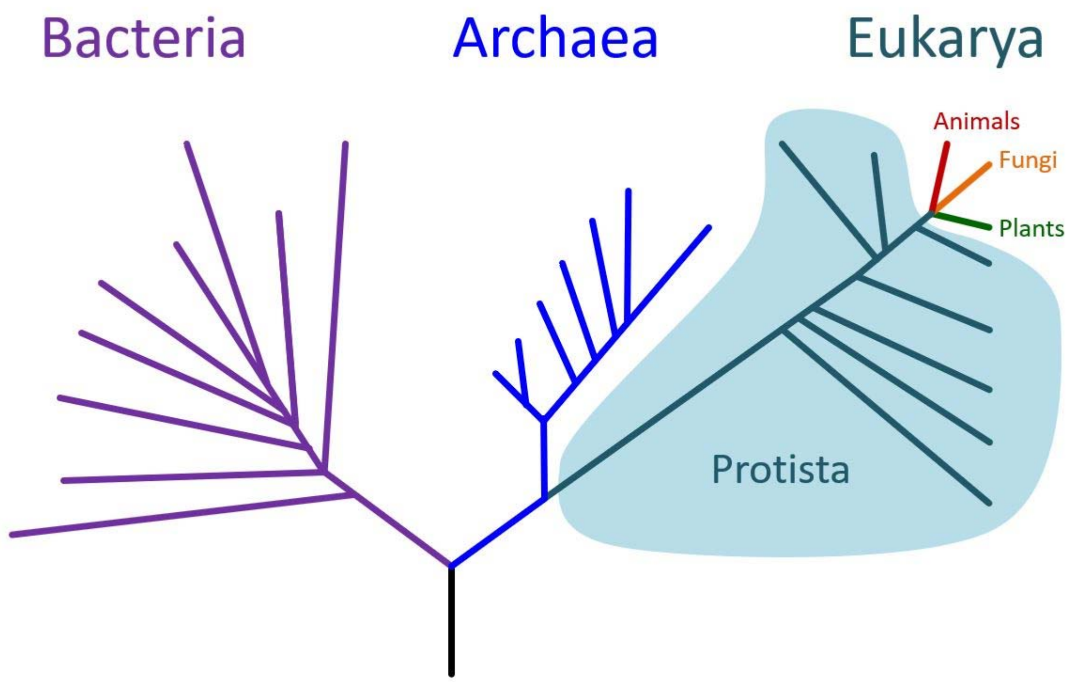

Figure 4-7: The current Tree of Life. The currently accepted hypothetical relationships between the three domains of living things. Bacteria, Archaea, and Eukarya (eukaryotes like you and me) are all thought to be descended from a common ancestor that lived billions of years ago.

Indeed, the entire Tree of Life is a nested hierarchy. We're all related. Darwin suspected this, and his theory predicted the phylogenetic trees that scientists have generated from the observations and other data available to us. In one of the most often-quoted passages from the *Origin*, he demonstrates the sense of wonder that all biologists have when contemplating the diversity of living forms.

"There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved." - Charles Darwin, 1859.